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A carrier of the mosaic disease

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(with plate 7)

Introduction

The symptoms and general character of the mosaic disease of tobacco and other solanaceous plants are becoming very well known through the work of Mayer (1886), Sturgis (1900), Woods (1899, 1902), Lowe (1900), Iwanowski (1903), Hunger (1905), Clinton (1908), Westerdijk (1910), Peters (1912), Allard (1914, 1915, 1916, 1917), Chapman (1913, 1916), Jensen (1913), and Freiberg (1917).

The disease has been observed on all varieties of *Nicotiana Tabacum*, on several of the more distinct varieties of tomato, on *Petunia violacea*, on *Physalis* (two distinct garden species), on *Datura Stramonium* and *D. Tatula*, on *Hyoscyamus niger*, on *Solanum nigrum* and *S. carolinense* and on several of the more distinct varieties of *Capsicum*. It has been transferred to all these from infected *N. Tabacum*. To this list should be added now *Solanum aculeatissimum*, the apple of Sodom, an infected plant of which was brought from Florida to the greenhouse of Columbia University in the winter of 1915.

According to Allard (1914) the following symptoms are characteristic of different phases of the disease at one or another stage in the infection: (1) partial or complete chlorosis, (2) curling of the leaves, (3) dwarfing and distortion of the leaves, (4) blistered or

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"Savoyed" appearance of the entire plant, (5) mottling of the leaves with different shades of green, (6) dwarfing of the entire plant, (7) dwarfing and distortion of the blossoms, (8) blotched or bleached corollas (in *N. Tabacum* only), (9) mosaic sucker growth, (10) death of tissue (sometimes very marked in *N. rustica*). To these should be added the narrowing of the leaves or frenching and their sometimes uniformly lighter or more yellowish green color.

In attempting to infect the alkekengi or bladder cherry (*Physalis Alkekengi*) I have found that although this plant when inoculated does not show any of the above visible symptoms, it may, nevertheless, become a carrier of the disease in the fullest sense, for I have infected *N. Tabacum* and the apple of Sodom with the juice of plants of the alkekengi which appeared to be entirely free from mosaic.

Allard reports (1914) that he has readily transferred the disease from tobacco to two distinct garden species of *Physalis*, which then showed the general symptoms of the disease, but he does not tell us what species of *Physalis* he used.

As grown by me the alkekengi certainly shows none of the ordinary symptoms, the plants remaining healthy in appearance for indefinite periods, after inoculation with the juice of diseased tobacco or apple of Sodom.

Allard (1917) reports some very interesting experiments on the behavior of the mosaic disease in *N. glauca*. He inoculated this species from diseased plants of *N. Tabacum* and found that the symptoms were confined to a sparse and indistinct mottling along the veins of some of the leaves. This mottling in some instances was too faint to be detected readily, except in transmitted light. Eight of these plants which showed these symptoms more clearly were tested by injecting the expressed sap of each into a series of plants of *N. Tabacum*. The sap of all proved exceptionally virulent, producing in most instances 100 per cent. of infection in each lot of ten plants. After the initial expression of the disease in *N. glauca*, Allard reported that the symptoms gradually became more attenuated, until they were barely distinguishable. In July three of these plants were cut back severely and were immediately transplanted to the field. Growth was resumed, but no symptoms of the mosaic disease whatever could be detected. However, inoculation tests demonstrated that the sap of these plants contained the infective principle of the disease. These plants were again taken from the field and transplanted into the greenhouse for the winter. Although growth appeared normal and symptoms of the mosaic disease could not be detected with certainty, experiments showed repeatedly that the infective principle of the disease was still present in the expressed sap. Allard further shows that when scions of the immune species, *N. glutinosa*, are grafted upon mosaic-diseased plants of *N. Tabacum* the infective principle of the disease may pass into *N. glutinosa* without the subsequent development of symptoms in it.

These experiments bear an interesting relation to my own observations on the alkekengi as a carrier of the disease. A so-called carrier of the disease is, first, an organism which through acquired toleration continues to harbor the germ or virus after recovery from the diseased condition; or second, one which through natural toleration may acquire and transmit the germ or virus without itself showing any symptoms or suffering in any way from the disease. A third type of carrier is found in those organisms which are immune, but may passively transmit a disease (as does *Abutilon arboreum* in Baur's grafting experiments), without necessarily becoming a seat for the multiplication of the germ or the increase of the virus. See Baur (1906).

MATERIAL AND METHODS

I have used two species of plants as a source of the mosaic disease, namely:

1. Apple of Sodom (*Solanum aculeatissimum*). The first plant of this species showing the mosaic disease was brought from Florida by Professor Harper in December, 1915. So far as I am aware this plant has not hitherto been reported as showing mosaic, though there is of course every reason to suppose that most of the species of *Solanum* are susceptible. The symptoms in apple of Sodom include all those enumerated above.

2. Tobacco (*Nicotiana Tabacum*). I have used the juice of mosaiced plants of the tobacco, kept as stock cultures in the greenhouse of Columbia University.

The juice for inoculation was procured by crushing the leaves. The inoculations were made in several different ways as follows:

No. 1. One stab in each node. In addition to the puncture the four upper leaves were rubbed on both surfaces with the same inoculum used for the needle stab.

No. 2. Five stabs on stem in the following places: one at the tip, one at the base, and three at equal distances between tip and base. Besides these punctures the five upper leaves were rubbed on both surfaces with the same inoculum as used for the stabs.

No. 3. Four stabs: one in the growing tip of stem, and three additional punctures on each in the base of the three upper young leaves near the midrib.

No. 4. Four stabs: one in growing tip of stem, one in middle of stem, a third in its base, and a fourth on the youngest leaf near the midrib.

No. 5. Three stabs on the stem: one in growing tip, one in the middle, and another one near the base of the stem.

No. 6. Four stabs: one in the growing tip of the stem, another in the middle of the stem, the third and fourth on the base of the upper two young leaves near the midrib.

No. 7. One stab in the growing tip of the stem.

No. 8. Two stabs: one in the middle of the stem and another in the blade of the youngest leaf.

EXPERIMENTS

1. *Inoculation of the alkekengi with juice of infected apple of Sodom plants.*

On May 21, forty-eight young plants (3–5 inches high) of the alkekengi were transplanted into five and a half inch pots from the garden and brought into the greenhouse. These were entirely free from mosaic disease and produced fine new growths in two weeks' time.

On June 5, nine plants out of the forty-eight were inoculated with the juice of *S. aculeatissimum* having the mosaic disease. I used method No. 1 in this experiment. No symptoms of the disease appeared in any of these plants. They were entirely indistinguishable from the controls. On June 27 these same nine plants were inoculated again by the same method as before. On

July 16 each plant was examined carefully, but there was no visible evidence of the disease.

On June 25 another series of inoculations with juice of diseased tobacco plants was made on fourteen healthy plants of the alkekengi. These plants were inoculated by method No. 2. After four weeks, although growth continued normally, they showed no symptoms of the disease.

The same experiment was repeated with another series of mature plants of the alkekengi (10–12 inches high). On August 4, twenty of these plants were inoculated with the juice from diseased *S. aculeatissimum*, another series of twenty plants were inoculated with the juice of diseased *N. Tabacum*. Method of inoculation No. 2 was used. After a period of thirty days no symptoms of the disease had appeared on the plants in these two series of experiments. See FIG. 1.

2. *Transfer of mosaic from the apple of Sodom to the alkekengi and then to tobacco*

It occurred to me that the plants might carry the disease, though not showing symptoms, and I inoculated plants of *N. Tabacum* and apple of Sodom with the juice from the alkekengi plants which had been inoculated from the apple of Sodom apparently without results.

TABLE I

SUMMARY OF EXPERIMENT NO. 2

No.	Date of inoculation	First symptom	Incubation period, days	25 days after inoculation
1	July 16	July 23, mosaic on the first new leaf	7	Disease developing
2	" "			No reaction
3	" "	July 24, mosaic on the first new leaf	8	Disease developing
4	" "	July 25, mosaic on the first new leaf	9	" "
5	" "	July 24, mosaic on the first new leaf	8	" "
6	" "			No reaction
7	" "	July 23, mosaic on the first new leaf	7	Disease developing
8	" "	July 24, mosaic on the first new leaf	8	" "
9	" "	July 25, mosaic on the first new leaf	9	" "
10	" "			No reaction
11	" "	July 23, mosaic on the first new leaf	7	Disease developing
12	" "			No reaction
13	" "			" "

On July 16 thirteen young healthy plants of *N. Tabacum* (six- to ten-leaf stage) were inoculated with the juice of the *P.*

Alkekengi which had been inoculated on June 5 and June 27 with the juice of mosaiced leaves of apple of Sodom. In this experiment inoculation method No. 3 was used. July 23, experimental plants 1, 7 and 11 showed mosaic on the first new leaves which were just appearing. July 24, plants 3, 5 and 8 also showed mosaic on the first new leaves. Finally on July 25, plants 4 and 9 exhibited mosaic on the first new leaves and these plants continued diseased, but plants 2, 6, 10, 12 and 13 did not show any symptoms whatever. Eight plants were left as controls and at the end of twenty-five days they showed no symptoms of mosaic· See TABLE I and FIG. 2.

3. *Transfer of mosaic from the tobacco to the alkekengi and then back to the tobacco*

I next tested plants of the alkekengi of the series which had been inoculated with mosaic from diseased tobacco plants with respect to their power to infect tobacco.

July 22, six young healthy tobacco plants (six- to eight-leaf stage) were inoculated with the juice of the alkekengi which showed no symptoms of the disease, although they had been inoculated with the juice of diseased tobacco on June 25. This inoculation was made by method No. 3. July 28, plant 3 showed mosaic on the first new leaf. July 29, plant 1 showed mosaic on the first new leaf. July 30, plants 2 and 5 showed mosaic on the first new leaf, but plants 4 and 6 did not show symptoms of the disease. For this experiment six control plants were kept, which after twenty-five days showed no mosaic.

The experiment was repeated in the period from August 8 to September 2.

August 8, twelve young healthy tobacco plants (six- to ten-leaf stage) were inoculated by method No. 4. August 15, plant 10 showed mosaic on the first new leaf. August 16, plants 7 and 14 showed mosaic on the first new leaves. August 17, plants 9, 11, 15 and 16 showed mosaic on the first new leaves. August 18, plants 12 and 18 showed mosaic on the first new leaves. August 19, plant 17 showed mosaic on the first new leaf.

All of the inoculated plants developed the disease except plants 8 and 13 which did not show any symptoms. In this experiment twelve plants were kept as controls and after twenty-five days they were found to be free from any symptoms of mosaic. See TABLE II.

TABLE II

SUMMARY OF EXPERIMENT NO. 3

No.	Date of inoculation	First symptoms	Incubation period, days	25 days after inoculation
1	July 22	July 29, mosaic on the first new leaf	7	Disease developing
2	" "	July 30, mosaic on the first new leaf	8	" "
3	" "	July 28, mosaic on the first new leaf	6	" "
4	" "			No reaction
5	" "	July 30, mosaic on the first new leaf	8	Disease developing
6	" "			No reaction
7	Aug. 8	Aug. 16, mosaic on the first new leaf	8	Disease developing
8	" "			No reaction
9	" "	Aug. 17, mosaic on the first new leaf	9	Disease developing
10	" "	Aug. 15, mosaic on the first new leaf	7	" "
11	" "	Aug. 17, mosaic on the first new leaf	9	" "
12	" "	Aug. 18, mosaic on the first new leaf	10	" "
13	" "			No reaction
14	" "	Aug. 16, mosaic on the first new leaf	8	Disease developing
15	" "	Aug. 17, mosaic on the first new leaf	9	" "
16	" "	" " " " " " " "	9	" "
17	" "	Aug. 19, mosaic on the first new leaf	11	" "
18	" "	Aug. 18, mosaic on the first new leaf	10	" "

4. *Inoculation of the tobacco with juice of healthy alkekengi plants*

To prove that the juice of uninoculated plants of the alkekengi will not produce the disease in tobacco twelve healthy young *N. Tabacum* plants (ten- to eleven-leaf stage) were inoculated on September 10 with the juice of the leaves of healthy *P. Alkekengi* by method No. 3, the same which was used in experiment No. 2. After thirty days two new leaves or more appeared on each plant but did not show any symptoms of the disease.

5. *Comparison of inculation periods*

To compare the length of the incubation period in my transfers through *P. Alkekengi* with the ordinary incubation period when tobacco is inoculated with juice from diseased tobacco, a series of inoculations was made using methods Nos. 4, 7, and 8; twenty plants of *N. Tabacum* were used in each of the three series. The first series were inoculated on March 28 by method No. 8, the plants having eight to ten leaves. The second series were inoculated on April 5 by method No. 7, the plants having five to seven leaves.

The third series were inoculated on August 10 by method No. 4, the plants having seven to eight leaves. Forty-eight of these showed the symptoms of disease. The incubation period was from six to seven days in each of the series. The mosaic symptoms always appeared on the first or second new leaves that were formed after inoculation. Fifteen controls were kept in each experiment and after twenty-five days they were found to be in a healthy condition. The incubation period is seen to be much the same in all the experiments:

In experiment No. 2, from 7 to 9 days;
In experiment No. 3, from 7 to 11 days;
In experiment No. 5, from 6 to 10 days.

This result agrees with the observations of other authors on the length of the incubation period. In each experiment the mosaic was observed on the first or second new leaf which appeared after inoculation.

The appearance of the mosaic leaves of apple of Sodom and tobacco, infected through the alkekengi, is the same in design and coloring (i. e., distribution of the dark green with relation to the vein, etc.) as in direct infection from tobacco to tobacco.

There can be no question that the virus induces the same symptoms after passing through the apparently immune plant as when transferred directly from one susceptible plant to another. The affected plants developed the disease on all new leaves which appeared after inoculation.

6. *Transfer of mosaic from the apple of Sodom to the alkekengi and then back to the apple of Sodom*

The transfer through *P. Alkekengi* from apple of Sodom to apple of Sodom is equally easy.

June 23, ten young healthy plants of apple of Sodom (3–4 inches high) were inoculated with the juice from the leaves of the same plants of *P. Alkekengi* (inoculated from apple of Sodom) which were used in experiment No. 2 as a source for the inoculation of tobacco. I used method No. 5 for this inoculation. June 30, plants 2 and 6 showed mosaic on the first new leaves. July 1, plant 4 showed mosaic on the first new leaf. July 2, plants 7 and

10 showed mosaic on the first new leaves. July 3, plant 1 showed mosaic on the first new leaf. These six plants developed the disease, but plants 3, 5, 8 and 9 showed no symptoms.

On July 20, the same experiment was repeated with another series of ten young healthy plants of apple of Sodom 4–5 inches high. July 29, plant 12 showed mosaic on the first new leaf. July 30, plants 11 and 13 showed mosaic on the first new leaves. July 31, plants 14 and 16 showed mosaic on the first new leaves. August 1, plants 19 and 20 showed mosaic on the second new leaves. Plants 15, 17 and 18 showed no symptoms.

Ten plants were kept in each experiment as controls and after twenty-five days they were found to be in healthy condition.

TABLE III

SUMMARY OF EXPERIMENT NO. 6

No.	Date of inoculation	First symptom	Incubation period, days	25 days after inoculation
1	June 23	July 3, mosaic on the first new leaf	10	Disease developing
2	" "	June 30, mosaic on the first new leaf	7	" "
3	" "			No reaction
4	" "	July 1, mosaic on the first new leaf	8	Disease developing
5	" "			No reaction
6	" "	June 30, mosaic on the first new leaf	7	Disease developing
7	" "	July 2, mosaic on the first new leaf	9	" "
8	" "			No reaction
9	" "			" "
10	" "	July 2, mosaic on the first new leaf	9	Disease developing
11	July 20	July 30, mosaic on the first new leaf	10	" "
12	" "	July 29, mosaic on the first new leaf	9	" "
13	" "	July 30, mosaic on the first new leaf	10	" "
14	" "	July 31, mosaic on the first new leaf	11	" "
15	" "			No reaction
16	" "	July 31, mosaic on the first new leaf	11	Disease developing
17	" "			No reaction
18	" "			" "
19	" "	Aug. 1, mosaic on the second new leaf	12	Disease developing
20	" "	Aug. 1, mosaic on the second new leaf	12	" "

7. *Inoculation of the apple of Sodom with the juice of healthy alkekengi plants*

To prove that the juice of uninoculated plants of *P. Alkekengi* will not produce the disease in the apple of Sodom, twelve healthy young plants of apple of Sodom (5–6 inches high) were inoculated on September 12 with the juice of the leaves of healthy *P. Alke-*

kengi by the method used in experiment No. 6. After a period of four weeks two or three new leaves had appeared on each plant but no symptoms of the disease had appeared.

8. *Transfer of mosaic from the tobacco to the alkekengi and then to the apple of Sodom*

To make the evidence still more clear that *P. Alkekengi* is a carrier, I tried an inoculation of the apple of Sodom with the juice of *P. Alkekengi* used in experiment No. 3, that is from plants inoculated from tobacco. The experiment is the reverse of experiment No. 2.

August 20, twelve young healthy plants of apple of Sodom (4–5 inches high) were inoculated with the juice of the leaves of *P. Alkekengi* which had been inoculated with the juice of mosaic leaves of *N. Tabacum.* Four punctures were made in each plant by method No. 6. August 30, plants 2, 3 and 10 showed mosaic on the first new leaves. August 31, plants 1, 9 and 11 also showed mosaic on the first new leaves. September 1, plant 5 showed mosaic on the second new leaf. September 2, plant 7 showed mosaic on the second new leaf. These eight plants developed the disease, but plants 4, 6, 8 and 12 did not show any symptoms.

TABLE IV

SUMMARY OF EXPERIMENT NO. 8

No.	Date of inoculation	First symptoms	Incubation period, days	25 days after incubation
1	Aug. 20	Aug. 31, mosaic on the first new leaf	11	Disease developing
2	" "	Aug. 30, mosaic on the first new leaf	10	" "
3	" "	" " " " " " " "	10	" "
4	" "			No reaction
5	" "	Sept. 1, mosaic on the second new leaf	12	Disease developing
6	" "			No reaction
7	" "	Sept. 2, mosaic on the second new leaf	13	Disease developing
8	" "			No reaction
9	" "	Aug. 31, mosaic on the first new leaf	11	Disease developing
10	" "	Aug. 30, mosaic on the first new leaf	10	" "
11	" "	Aug. 31, mosaic on the first new leaf	11	" "
12	" "			No reaction

In this experiment twelve controls were kept and after twenty-five days they were found to be in healthy condition. See TABLE IV and FIG. 3.

9. *Inoculation of the apple of Sodom with juice of infected tobacco plants*

Before making the above experiments with the alkekengi I had already satisfied myself as to the relation of the mosaic of tobacco to that of the apple of Sodom.

Forty young healthy plants of apple of Sodom (4–6 inches high) were used in each of the two series. The first series was inoculated on March 27 with juice from diseased apple of Sodom. The second series was inoculated on March 25 with juice from diseased tobacco. These inoculations were made by method No. 5. In the first series thirty-three plants showed mosaic. The incubation period was from eight to ten days. In the second series thirty-six plants showed mosaic. The incubation period was from seven to twelve days. In every case the mosaic symptoms appeared on the first or second new leaves that were formed after inoculation. The incubation period was much the same in all these experiments. Twenty-five controls were kept and after thirty days they were found to be in healthy condition.

The appearance of the mosaic leaves of apple of Sodom, produced by infection from the carrier, *P. Alkekengi* (which had been inoculated from apple of Sodom or from tobacco) is the same as in the case of direct infection from tobacco or apple of Sodom in the distribution of the dark green with relation to the veins, in the blistering, etc. There can be no question that the virus induces the same symptoms after passing through the apparently immune plant to another as when transferred directly from one susceptible to the disease.

10. *Reinoculation of tobacco plants*

The *N. Tabacum* plants inoculated in experiments 2, 3, and 4, which did not take the disease, were later used for further inoculations with virus from the diseased tobacco which had been inoculated from *P. Alkekengi*. September 10 the fourteen plants of *N. Tabacum* were inoculated by method No. 1. September 18, plants 3 and 5 showed the mosaic on the first new leaves. September 19, plants 7 and 11 also showed the mosaic on the first new leaves. September 20, plants 8, 10 and 12 showed the mosaic. September 21, plants 2, 6 and 9 showed the mosaic. September

22, plant 13 showed the mosaic on the second new leaf. These eleven inoculated plants developed the disease, but plants 1, 4 and 14 did not show any symptoms.

It is evident that the failure to infect these plants in the earlier inoculations was due to the uncertainties of the method of inoculation. Twelve of these same plants were kept as controls (four plants which had been used in experiment No. 2, five plants from experiment No. 3 and the other three plants from experiment No. 4). All of the controls but one remained in a healthy condition. The results show that the chances of accidental inoculations in the greenhouse where the work was carried on were very small. These control plants with one exception had remained uninfected for over two months.

11. *Reinoculation of apple of Sodom plants*

The same test was made on the plants of the apple of Sodom which had remained healthy after inoculation in the earlier experiments.

September 13, the twelve plants of apple of Sodom of experiments 6, 8 and 9, which had failed to develope the disease were inoculated by method No. 6 with juice from diseased tobacco which had been inoculated from *P. Alkekengi.* September 21, plants 8 and 11 showed the mosaic on the first new leaves. September 22, plants 7 and 6 showed the mosaic as above. September 23, plants 2, 4 and 5 showed the mosaic as above. September 24, plant 9 showed the mosaic as above. September 25, plant 12 showed the mosaic on the second new leaf.

Nine plants developed the disease, but plants, 1, 3 and 10 did not show any symptoms.

SUMMARY

Physalis Alkekengi is found to be a carrier of the mosaic disease without itself showing any symptoms. The experimental results were as follows:

1. Thirty-four healthy plants of *Physalis Alkekengi* were inoculated with juice of mosaic-diseased plants of *N. Tabacum* and showed no symptoms. To test the method of inoculation and the virulence of the disease sixty young healthy plants of *N.*

Tabacum were inoculated with juice of the mosaic-diseased tobacco and forty-eight of these plants showed the disease.

2. The same test was made with the juice of mosaic-diseased *Solanum aculeatissimum* on twenty-nine healthy plants of *P. Alkekengi*, and none showed any symptoms of the disease. Of forty healthy plants of *S. aculeatissimum* inoculated with juice of mosaic-diseased *S. aculeatissimum* thirty-three plants showed the disease.

3. Of thirty-one healthy plants of *N. Tabacum* inoculated with juice from leaves of *P. Alkekengi* which showed no symptoms of mosaic but had been inoculated from diseased tobacco or *S. aculeatissimum*, twenty-two plants showed typical mosaic disease. Of twelve young healthy plants of *N. Tabacum* inoculated with juice from leaves of *P. Alkekengi* which had not been inoculated none showed the disease.

4. Of thirty-two healthy plants of *S. aculeatissimum* inoculated with juice from leaves of *P. Alkekengi* which showed no symptoms of mosaic but had been inoculated from diseased tobacco or *S. aculeatissimum*, twenty-one plants showed mosaic also. Of twelve young healthy plants of *S. aculeatissimum* inoculated with juice from leaves of *P. Alkekengi* which had not been inoculated, none showed the disease.

5. Experiments have shown that the mosaic diseases of *S. aculeatissimum* and *N. Tabacum* are similar with respect to the symptoms and incubation periods.

6. The juice from diseased *N. Tabacum* when passed through *P. Alkekengi* to *N. Tabacum* has produced the disease in 80 per cent. of the inoculations on healthy plants of *S. aculeatissimum* or *N. Tabacum*. It is evident that there is no marked weakening of the virus by the carrier *P. Alkekengi*.

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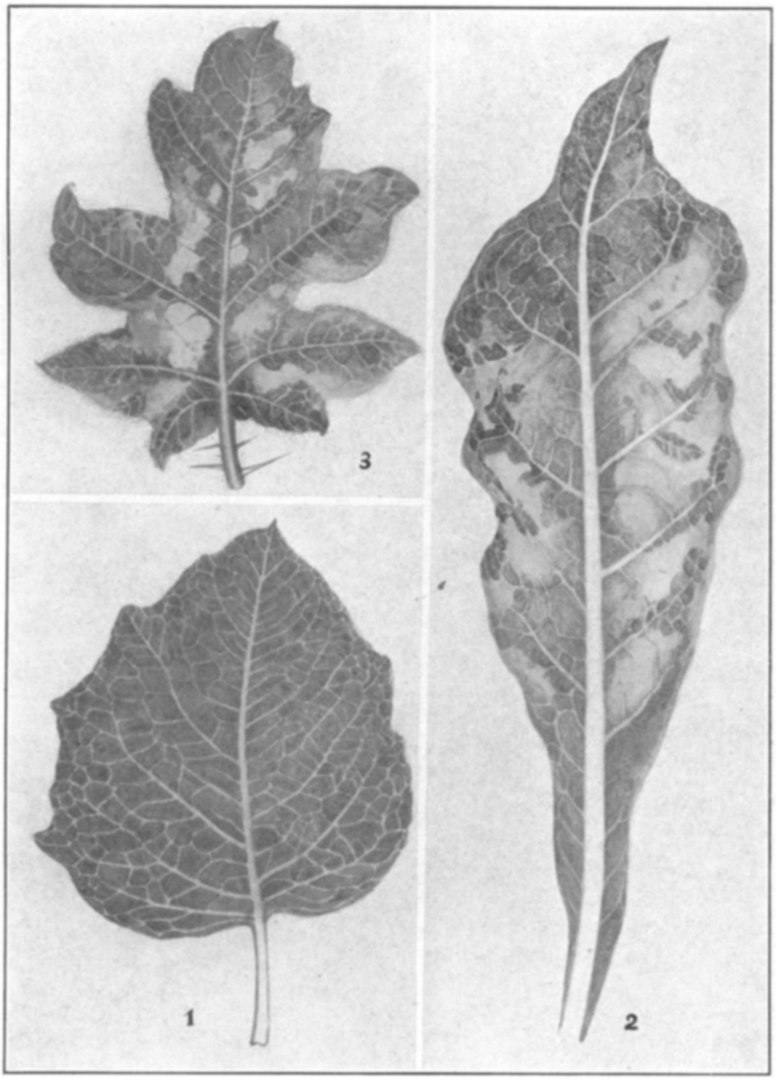

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Explanation of plate 7

FIG. 1. Typical leaf of *Physalis Alkekengi*, the carrier of the mosaic disease, inoculated with the juice of the leaves of *Solanum aculeatissimum* having mosaic disease but not showing any symptoms of the disease.

FIG. 2. Typical mosaic leaf of *Nicotiana Tabacum*, inoculated with the juice of the leaves of *Physalis Alkekengi* which had been inoculated with the juice of mosaic leaves of *Solanum aculeatissimum*.

FIG. 3. Typical mosaic leaf of *Solanum aculeatissimum*, inoculated with the juice of *Physalis Alkekengi* which had been inoculated with the juice of mosaic leaves of *Nicotiana Tabacum*.